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MORPHOLOGY OF THE EXOSKELETON OF CAPNOCHROA FULIGINOSA (MELSHEIMER) (Alleculidae)

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Introduction

The order Coleoptera is among the best known of all groups of insects and, at the same time, it is equally true that the morphological details of many families within this order are poorly known. Tanner (1927) complained that "students have been content, in most cases, to place these insects (beetles) upon pins and treat them as priceless objects to be admired and not studied by means of microscopic dissection." Fortunately, this statement does not have such universal application today.

In the introduction to his very comprehensive morphological study of the family Staphylinidae Blackwelder (1936) said this: "morphology is one of the important foundations of classification because it supplies the easiest and most usable key to the relationships between individuals". No true system of natural classification can be attempted without this basic and comprehensive knowledge.

Additional studies of the entire external morphology of single species of Coleoptera have been completed within the last twenty-five years by Campau (1940). Bryson and Dillon (1941), Rings (1942), Butt (1944) and Bostick (1945) to mention part of a list which is all too short considering the large number of beetle families and the wealth of information still uncovered. It is certainly evident that the stage has not arrived where one can maintain that the usefulness of morphological characters has

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been exhausted and therefore the solution to the question of relationships between individuals must be sought elsewhere.

The purpose, then, of this particular study is to supply additional information on the morphology of the monobasic genus *Capnochroa* LeConte of the family Alleculidae with a view toward supplementing the present limited knowledge of this family and its classification as well as contributing to the morphological knowledge of Coleoptera in general.

Methods and materials

A series of ten specimens of *Capnochroa fuliginosa* (Melsheimer) obtained from the Arnett collection were used for this study. Most of the specimens were collected in New York State.

This is the sole species in the genus according to Borchmann (1910), and was described by Melsheimer in 1846.

Gross features of the anatomy were obtained from studying specimens mounted on pins. Two females and two males were dissected and studied according to the following method: the beetle was placed in an ordinary small porcelain crucible containing a 10% solution of KOH and was heated in this solution for about one minute. This was sufficient to soften the body and permit easy separation of the body regions. The procedure then followed was to remove the head first and place the remainder of the specimen in a vial of 95% alcohol until work on the head capsule and appendages was completed. Further heating in KOH was usually necessary in order to dissect the mouthparts and study the head capsule thoroughly. The same method was employed for the dissection and study of the prothorax and appendages, pterothorax and appendages, abdomen and genitalia. The various parts were dissected in 95% alcohol and stored in vials of the same. This made it possible to move the parts in any desired position while studying them. Drawings were made before and after dissection of all views necessary to show the structures clearly and the relation of the various parts to each other. All work was done using a binocular dissecting microscope with magnifications of 15X, 45X, and 120X. This range of magnification together with the above mentioned advantage of working with alcohol preserved specimens seemed most satisfactory for this particular study.

The terminology, abbreviations and, in general. the interpretations of Snodgrass (1935) were followed throughout the work with the exception of the section on genitalia. Here the work of Lindroth (1957) was used, for the most part, as the basis for interpreting and naming the structures found.

Description Of **CAPNOCHROA FULIGINOSA** (MELSHEIMER)

(Figure 1)

Capnochroa fuliginosa (Melsheimer) is a moderately large beetle. The females average 12 mm. in length and 5 mm. in width. The males, less robust, measure, on the average, 11 mm. or a little more in length and 4.5 mm. in width. The general appearance of this species is that of an elongate, elliptical, convex beetle with a prognathus head. The color is dark chestnut brown with black patches intermixed particularly on the pronotum and venter. The pubescence is very fine, short, and flavate. These flavate hairs are dense on the pronotum giving a dull appearance and rather sparse on the elytra resulting in a shiny appearance. The legs are long and slender and do not vary much in this respect in the two sexes. Each segment of the leg is densely clothed on the ventral surface with short flavate hairs in the male. The antennae are long, filiform to subserrate, and about half the length of the body.

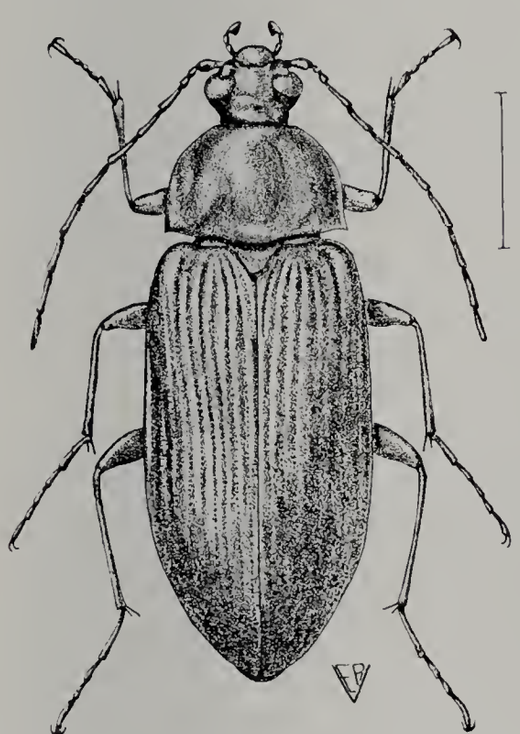

Figure 1.—*Capnochroa fuliginosa* (Melsheimer), female

Head

(Figures 2 and 3)

Dorsal aspect.—(Figure 2) One large sclerite, the epicranium, extends from the *occipital suture* to the clypeus. The sutures are obliterated which might divide this area into distinct frons, vertex, and genae. The horseshoe-shaped occipital arch forms the posterior aspect of the head dorsal to the *foramen magnum*. The dorsal portion of the arch is referred to as the *occiput* and the lateral parts, the *postgenae*. The narrow area between the dorsal mandibular articulation and the eye represents the *gena* (fig. 3). The dorsal and dorso-lateral aspect can be considered the *vertex*. The *epistomal suture* marks the distal extremity of the *frons*, but, there being no frontal suture, the posterior extent of the frons can only be estimated as the area proximad of the epistomal suture, between the eyes and distal to the area generally outlined above as the vertex.

The *clypeus* is a single sclerite joined to the front by the epistomal suture. A tough membranous strip, the *anteclypeus*, forms the anterior

margin and overlaps the ridge on the labrum to form the clypeolabral junction.

The moderately large *eye* is situated in the median part of the lateral aspect of the head. There is a marked emargination in the dorsal third of the anterior margin. The raised *antennal ridge* projects into this emargination. The *oculata* is present as the part of the head capsule surrounding the ocular fossa and over which the lateral borders of the eye are placed. The oculata therefore forms a narrow internal shelf for the eye. The hemispherical facets are moderately small in size. Ocelli are absent.

Ventral aspect.—(Figure 3) The median area of the ventral surface of the head capsule is occupied by a triangular sclerite, the *gula*, which closes the foramen magnum with its base and has its lateral borders converging anteriorly to form the single *subgenal suture* which in turn connects anteriorly with the submentum. The lateral areas of the head capsule represent the *subgenal* parts of the epicranium. A ridge, the *crassa*, is found on the anterior ental surface of the head capsule extending from the mesal side of the ventral mandibular articulation to the submentum.

Tentorium.—(Figure 3) The *anterior tentorial arms* arise from the internal *subgenal ridge* just proximad of the dorsal mandibular articulation and between it and the antennal fossa. This site of origin is characteristic of the more generalized pterygote insects according to Snodgrass (1935). The anterior arms pass posteriorly and ventrally to join the *posterior arms;* the short *dorsal arms* are given off a little distad of the origin of the anterior arms. The posterior arms of the tentorium arise just proximad of the apex of the gula as indicated externally by a distinct, though shallow unevenness in the gular suture, the *posterior tentorial pit.* The posterior arms extend caudally to the edge of the foramen magnum and are united to the gular suture by membrane. The narrow H-shaped *tentorial bridge* is formed dorsal to the middle of the gula where the tentorial arms of opposite sides fuse.

Antennae.—(Figure 1) The eleven segmented *antennae* are inserted beneath the elevated antennal ridge of the epicranium just anterior to the emargination of the eye. They are nearly half the length of the body, somewhat compressed and filiform to sub-serrate. The three basal segments differ from the distal eight. The basal segment is the same length in both male and female, is elongate, cylindrical and as long as segments two plus three in the male, but not quite so in the female where the third segment is longer. The usual projection from the ventral aspect of the antennal fossa, the antennifer, supports the antenna. The second segment is half the length of the third in the female, less than half in the male, and of smaller diameter than the basal segment in both sexes. The third segment expands from its proximal end to the distal reaching at the apex the diameter of

the basal segment. This third segment is longer on its outer edge than on the inner apparently allowing for more freedom of movement. The first and third segments are evenly covered with short setae; the second more sparsely so. The dense system of pores characteristic of the remaining segments is absent from the three basal segments. Segments four to ten are similar in appearance and size. These segments are quite serrate in appearance in the male but more filiform in the female. The eleventh segment is filiform in both sexes and comes to an acute tip which is clothed with a few longer setae than the remainder of the segment. A paler elliptical area extends back from the tip of segment eleven on the outer surface of the segment. This area is characterized by a density of minute setae, a few longer setae, and many small pores. This is probably a more highly specialized sensory area. Segments four to eleven have the entire surface covered with short setae interspersed with numerous large circular pits filled with a white substance.

Mouthparts

(Figures 4—10)

Labrum.—(Figures 4 & 5) The labrum is a broad, convex sclerite having a shallow sinuation in its anterior margin as well as a slight indentation at the center of this margin. The dorsal surface is clothed with both coarse and fine setae, more densely so toward and at the anterior margin. Near the proximal edge of the sclerite is a heavily sclerotized *ridge* (fig. 5) extending the width of the labrum marking the point of connection with the clypeus. The ventral surface is membranous and covered near the anterior margin with very fine hairs which become coarser at the margin. Proximally the membrane is continuous between the two laterally placed internal sclerites, *tormae*, and is continuous with the membrane of the inner surface of the clypeal region. The *epipharynx* projects posteriorly between the tormae as an irregular triangular lobe clothed densely with fine short hairs which are recumbent laterally but upright along the median line. A central depressed area on the ventral surface extends posteriorly about half the length of the labrum and is characterized by numerous circular pores of unequal size. An inverted T-shaped internal support lies dorsal to this depressed area in the center and extends posteriorly the same distance.

Mandibles.—(Figures 6 & 7) The mandibles lie posterior to the labrum and are prominent, heavily sclerotized and produced distally into curved, blunt, bilobed tips, the lobes of which are subequal in length and width. The expanded latero-basal area has a sparse covering of short bristles. The inner surface bears a large, sclerotized basal masticatory or *molar area* consisting of moderately narrow deeply cut vertical ridges. Arising from the

antero-ventral edge of this molar surface is an expansive membranous lobe, the *prostheca*, which continues to just short of the apex of the dorsal lobe of the mandible. The prostheca is noticeably clothed on its antero-mesal edge with numerous short, fine hairs. The mandible articulates with the head capsule by means of a dorsal and a ventral condyle. A crescent shaped *acetabulum* is found on the dorso-lateral base of the mandible and a spherical *condyle* on the ventro-lateral base. Articulation is made at these two points with the large dorsal crescent shaped *condyle* (fig. 3) on the gena immediately in front of the eye and antennal fossa and with the ventral hemispherical *acetabulum* (fig. 3) on the crassa.

Maxillae.—(Figure 8) The maxillae are located posterior to the mandibles. Each maxilla is made up of several sclerites forming the body of the maxilla, the galea, the lacinia and the maxillary palpus. The basal sclerite, the *cardo*, articulates at its proximal end with the crassa, is closely associated with the submentum and mentum mesally, and articulates distally with the stipes. The *stipes* is secondarily divided bearing the large galea and the slender, elongate lacinia on the distal portion and the palpifer on the lateral side of the proximal portion. The *lacinia* is a narrow lobe covered with fine hairs and ending in a tuft of longer fine hairs. It is bounded laterally by a small sclerite on each side and is joined to the galea only in the basal membranous area. The *galea*, the larger and longer of the two lobes ends in a stout tuft of fine hairs. Two chitinized bands partially encircle this lobe. The *palpus* is four segmented and joined to the stipes by the *palpifer*. The first segment is small, longer on the mesal side than the lateral side allowing more extensive lateral movement of the second segment. The second segment is longer than and has a greater diameter than the first; the diameter increases from base to apex. The third segment has a basal and apical diameter subequal to the respective measurements of the second, but is less than half as long as the second. The last segment is broadly expanded into a triangle in which the inner side is half as long as the outer and a little more than half the length of the apex. The three distal segments are clothed with short, strong setae. The basal segment has only a few setae near the apex on the mesal side.

Labium.—(Figure 9) The labium is made up of three sclerites: the submentum, mentum and prementum. The submentum and mentum together form the *postlabium*, and the prementum which bears the palpi and ligula is the *prelabium*. The *submentum* is rather firmly fixed to the head capsule and is connected with the apex of the gula by a short suture which represents the posterior portion of the submentum as explained by Williams (1938). The *mentum* is larger than the submentum and has its lateral borders produced posteriorly into a short projection on each side which clasps the anterior margin of the submentum. The sides of

the mentum are expanded entally to meet the ventralmost point of the sclerite supporting the hypopharynx. The *prementum* appears to be composed of at least three parts: a feebly sclerotized piece on the proximal ventral surface of the ligula between the bases of the palpi, and a lateral piece dorsal to each palpus. These lateral sclerites extend from the dorsal surface of the mentum to the proximal edge of the lateral extremities of the ligula. At the middle of each of these lateral sclerites, a narrow band passes down over the ventral surface of the *palpiger*. The labium terminates in a broad membranous, translucent T-shaped flap, the *ligula*, formed by the fusion of the glossae and paraglossae. The ligula is densely clothed on the dorsal and apical surfaces, and less densely on the ventral surface with fine recumbent hairs. Pores of various sizes are sparsely scattered on the ventral and dorsal surface apically as in the case of the ventral surface of the labrum. The palpiger bears the three segmented labial *palpus*. The first and second segments are quite similar in diameter and length. The terminal segment is not much longer than the first or second but is slightly expanded distally, compressed and arcuate. All three segments are sparsely covered with setae. The *hypopharynx* (fig. 10) is reduced to a small fleshy lobe very densely covered with short, fine, erect hairs. It projects dorsally from the center of a concavity on the dorsal surface of the labium. In this position it serves to force or hold food in the region of the molar grinding surfaces. The adoral surface of the hypopharynx is supported laterally and posteriorly by the sclerite known as the *hypopharyngeal suspensorium*.

Prothorax

(Figures 11 and 12)

Cervix.—The neck region or cervix is all membranous, no cervical sclerites present.

Pronotum.—(Figures 11 & 12) Dorsally the prothorax is very slightly convex, three-fourths wider than long, densely and finely punctate with the punctures narrowly separated and the interspaces finely alutaceous. The *basal angles* (fig. 1) are right, the *basal sinuations* (fig. 1) broad but shallow and the *basal fovea* (fig. 1) distinct though small. The sides of the pronotum are straight and parallel in about the basal half, then roundly converging to the apex which is about half as long as the base. The pronotum is inflexed laterally to form the hypomera (fig. 12) which is set off from the disk by the marginal ridge. Anteriorly the hypomera continues as far as the anterior foramen on the dorsal aspect and the *sterno-notal suture* on the ventral aspect. Caudad of the coxal cavities the hypomera

is prolonged mesally as a slender lobe which becomes somewhat membranous at the tip. The approximation of these hypomeral extremities at the midline of the body closes the coxal cavities behind. Both the anterior and posterior edges of the lobes are very sparingly set with setae. The caudal pronotal inflection is in the form of a triangular area on each side of the posterior foramen at the dorso-posterior corners. The punctuation and pubesecnce of the hypomera is like that of the disk of the pronotum except near the coxal cavities where both become sparse.

Prosternum.—(Figures 11 & 12) The sternite of the prothorax extends from the ventral border of the anterior foramen laterally to the sternonotal sutures and posteriorly to form the anterior borders of the *coxal cavities.* The median posterior prolongation of the prosternum forms the intercoxal process or the *spinasternum.* Entally this process is fused with the membrane lining the coxal cavities and it is from the floor of these cavities that the *sternal apophyses* or furcal arms arise. The prosternum is less heavily sclerotized and less densely punctate than the hypomera. A trochantin is not present on the prothorax.

Prothoracic legs. —(Figures 13 & 14) The *coxa* of the foreleg is distinct, spherical, reticulately strigulate and covered with very short, fine hairs set in small punctures. The lateral surface of the coxa extends internally to articulate with the distal end of an apophysis arising from the anterolateral corner of the pronotal disk. The articulation thus formed is quite flexible. The coxa has a groove which extends from the anterior trochanteral articulation mesally to the prosternal intercoxal piece permitting extensive movement of the trochanter in a dorso-ventral plane.

Trochanter.—(Figure 13) The trochanter is a short segment joined immovably to the femur and articulating with the coxa by means of a ball and socket arrangement held in place internally by muscle attachments and externally by a prominent condyle on the posterior surface of the coxa. The trochanter is covered with short, fine setae and about three longer setae on the ventral surface.

Femur.—(Figure 13) This is the stoutest segment of the prothoracic leg and equal in length to the tibia. It is nearly even in thickness throughout, only tapering somewhat at each end. Proximally it is fixed to the trochanter and also has a prominent rounded elevation at the proximodorsal edge which articulates with the corresponding depression in the coxa above the coxal condyle. A dorso-ventral groove at the distal end of the femur receives the head of the tibia and also extends proximally on the under surface of the femur a short distance making it possible for the tibia to be flexed back against the femur. The entire surface of the

femur is more or less reticulately strigulate and finely, evenly punctate with each puncture bearing a short seta.

Tibia.—(Figure 13) As stated above the tibia is as long as the femur. A distinct emargination is located on the ventral surface of the tibia just distad of the femoral articulation. The joint between the femur and tibia is dicondylic, the head of the tibia fitting between a condyle on each side of the femoral groove. This type of joint permits movement in one plane only. The tibia is slightly expanded at its distal end and also slightly longer on its anterior surface. The distal end of the tibia bears two large spurs, the *calcaria;* is encircled by smaller spurs which are probably stout setae and is attached by membrane to the basal segment of the tarsus. The calcaria are inserted in the membrane of the tip, one on the antero-ventral aspect of the tip; the other on the postero-ventral aspect. The small spurs which circle the tip are a little longer in the area between the calcaria. The entire surface of the tibia is minutely strigulate and clothed with moderately fine setae, evenly and closely set. A number of stout setae like those of the tip are scattered over the surface of the tibia.

Tarsus.—(Figure 13) The tarsus of the prothoracic leg is composed of five segments. The segments are slightly expanded at the distal end and longer on the dorsal than the ventral edge. The basal segment is only slightly shorter than the second, third, and fourth combined and similarly slightly shorter than the fifth segment. The proximal end of the basal segment is rounded and fitted into the membrane of the tip of the tibia. Just distad of this end and on the dorsal surface is an abrupt and deep indentation allowing maximum movement of the tarsus in a dorsal direction. The second, third and fourth segments are similar in size and shape. The third and fourth are somewhat shorter than the second and the fourth is less expanded distally than either the second or third. The fifth segment maintains the cylindrical shape of its proximal end to very near its distal end where it expands slightly to give attachment to the large claws on its dorsal aspect and the fleshy lobe, the empodium, on the ventral surface. The *claws* are laterally compressed, long, curved and tapered distally to sharp tips. From the inner face of each claw arise six or seven sharp teeth which increase in size from the first to the last. Ventrad of the claws lies the *unguitractor plate* (fig. 14) with the fleshy *empodium* at its distal end and the *tendon* of the retractor muscle of the claws attached to its proximal end. All of the tarsal segments are rather densely covered with setae, denser on the ventral surface and longer at the distal expanded ventral region. The rounded proximal end of the basal segment is glabrous. The fifth segment is more or less uniformly covered with setae throughout.

Pterothorax

(Figures 15-17)

Mesothorax.—(Figures 15-17) The mesothorax is connected to the prothorax by a membrane in which the *mesothoracic spiracles* are ventro-laterally situated. The *mesotergum* is considerably smaller than either the prothoracic or metathoracic terga. The dorsal aspect of the tergum is without distinguishable sutures. In general then, the posterior lobe which projects back over the metathorax is interpreted as the *scutellum;* the expanded part anterior to the scutellum, covered by the pronotum and bearing laterally the anterior notal wing process is the *prescutal area*, and the transverse sclerite ending laterally in the posterior notal wing process while joined to the scutellum ventrally by a lightly sclerotized v-shaped ridge is the *scutum.* A submarginal ridge, the *antecosta*, is also found at the anterior margin of the mesotergum. The scutellum, the only part seen when the elytra are in repose, is more heavily sclerotized than the other areas. The entire dorsal aspect except the anterior margin bears numerous moderately coarse setae.

The ventral aspect of the mesothorax is occupied by the *mesosternite*, a single sclerite which is separated from the membrane joining the prothorax and mesothorax by the narrow inflected *prepectus.* The prepectus is the anterior marginal sclerite of the mesothoracic pleura and sternum. It is divided into three sections by the *sterno-pleural sutures.* The mesosternum extends laterally to the suture just mentioned and forms the anterior margin of the coxal cavity. Posteriorly it forms the intercoxal process, the *spinasternum.* Internally this process is continued onto the floor of the coxal cavities. From this point a two-branched *apophysis* arises on each side. The shorter mesal arm of the apophysis ends in the sterno-pleural suture and the longer arm extends to the membrane between the pleuron and notum of the mesothorax.

The pleuron of the mesothorax is composed of the episternum and the epimeron separated by the *pleural suture.* The *episternum* is separated from the sternum by the sterno-pleural suture. Internally a strong *pleural ridge* corresponding to the external pleural suture extends from the coxal articulation dorsally to the pleural wing process and forms a brace between the wing and coxa. The episternum is finely and densely punctate along the prepectal margin becoming more coarsely and much less densely punctate posteriorly, and is finely strigulated throughout. Short, fine setae are borne by the punctures.

The *epimeron* of the mesothorax is the sclerite posterior to the pleural suture. It articulates with the trochantin at the antero-lateral extremity

of the coxal cavity. Thus the *mesocoxal cavities* are open laterally. Posteriorly it overlaps the episternum of the metathorax and its narrow medial edge lies under the antero-lateral extremity of the metasternum. The lightly sclerotized dorsal margin is continued anteriorly into the *wing process* of the episternum. The surface is evenly, sparsely punctate and finely strigulated. Internally a membranous fold extends from the posterior margin of the epimeron to its anterior margin but is not fused with the latter as it is with the dorsal, ventral and posterior margins of the sclerite. The *metathoracic spiracle* is situated in thinner membrane which is the mesal continuation of the fold just described.

The *basalare* is a small triangular sclerite located in the membrane anterior to the episternum close to the edge of the prepectus.

The *trochantin* of the mesothorax is a small feebly sclerotized rectangular sclerite which articulates with the epimeron by means of a blunt condyle and is closely associated with and moveable upon the coxa. It is finely strigulated and otherwise devoid of sculpturing or vestiture.

Mesothoracic legs.—(Figure 16) The mesothoracic legs are longer than the prothoracic legs and the segments less stout. The *mesothoracic coxa* is larger and more ovate than that of the prothorax. It bears a depression from the proximal to distal end along its postero-ventral aspect which receives the dorsal surface of the femur when the latter is flexed upward. The trochanter and its articulations are as described for the prothoracic legs. The femur is longer and less stout than that of the forelegs and nearly the basal half of the concave posterior surface is devoid of setae. Otherwise, the prothoracic and mesothoracic femora are quite alike. The mesothoracic tibia is longer than and more slender than that of the prothorax, but otherwise very similar to it. The two calcaria are similar in size and location to those of the prothoracic legs. The tarsal segments are quite like those of the forelegs being only somewhat longer and having a number of coarse setae interspersed among the normal finer setae on the ventral aspect.

Elytra.—(Figures 1, 18, 19) The elytra are four and one-half times longer than the prothorax, one-half more than the width of the prothorax and gradually dehiscent from about the middle. Each elytron is narrowly and gradually rounded at the tip. Basally the humerus forms on oblique angle with the base of the prothorax. The disk has distinctly impressed *striae* (fig. 1) with rounded punctures. The *intervals* (fig. 1) are moderately convex, finely and confusedly punctate with about five punctures in the width of one interval. The pubescence is fine and short over the whole elytron. The disk of the elytron has an acute and conspicuous lateral margin which is properly called the *dorsal ridge* of the epipleural fold. The inflexed portion beneath this ridge is the *epipleural fold* which tapers

from the humeral region to the apex of the elytron. The epipleura or narrow piece sometimes present along the edge of the elytron is absent in this species. The usage here of the terms dorsal ridge, epipleural fold and epipleura is in accordance with the original definitions as clarified by Arnett (1947). The elytron is connected to the mesothorax between the mesonotum and the mesepisternum by means of a membrane in which several irregularly shaped sclerites are situated. These are the *axillary sclerites* four of which appear present, as well as one distinguishable *median plate* between the second and third sclerites.

Metathorax.—(Figures 15–17) The metathorax is the largest thoracic segment and is closely united to the mesothorax anteriorly and the abdomen posteriorly. The *metatergum* is made up of five distinct areas, four fundamental to the tergum; one, a secondarily developed sclerite. The first tergal area is the *prescutum*, a lightly sclerotized area separated from the scutal areas by membrane and from the *antecosta* (fig. 20) of the metatergum by the *antercostal suture*. The prescutum is covered medially by the posterior lobe of the mesonotum. Two small irregular areas of sclerotization lie within the membrane laterad of the prescutum and function in connection with the axillary sclerites.

The *scutum* is divided into two areas by the *convergent sutures* or notaulices and these two scutal areas are separated mesally from the scutellum by the *scutoscutellar ridges* but are confluent with the scutellum laterally combining with it to form the *posterior notal wing process*. The entire surface of the scutum is finely strigulated and a restricted area of setae extends from near the posterior extremity of the scutoscutellar ridge in an oblique direction to the lateral margin of the scutum.

The central part of the metatergum extending from the anterior margin to the postnotal suture and expanding laterally to the postnotal wing processes is the *scutellum*. The median portion of the scutellum is elevated by a sort of out-folding of the tergum but no external groove or internal ridge is apparent to merit the designation of reversed notal suture. The surface of the scutellum is like that of the scutum but devoid of setae.

The *postnotum* is a secondarily developed sclerite caudad of the metatergum and separated from the latter by the postnotal suture. Posteriorly it is joined by a short membrane to the first abdominal tergite. Laterally it is reflected around the first abdominal spiracle and closely approximates the epimeron of the metathorax. The *postnotal plates* are enclosed by internal membranous ridges marked externally by narrow sclerotized borders.

The *metasternum* is the large sclerite that extends from the mesothoracic coxal cavities to the metathoracic coxal cavities. It bears three external

lines or secondary sutures which indicate infoldings or ridges. The first of these is in the midline from the posterior margin of the sclerite to just short of the anterior margin. The other two grooves are located one on each side of the midline and extend from its base obliquely cephalad but do not quite reach the sterno-pleural suture. The portion of the sternite posterior to this line is referred to as the *antecoxal piece*, the piece which overlaps partially the anterior aspect of the coxa and provides the degree of flexibility needed at this point. The oblique groove just described is incomplete; the antecoxal piece is continuous at its lateral extremity with the remainder of the sternite. Anteriorly the metasternum has a short median process, somewhat membranous on its ental surface, which comes in close proximity to the spinasternum of the mesosternum. The anterior corners of the metasternite articulate with the postero-ventral aspect of the mesepimeron. Laterally the sternite is separated from the metathoracic pleuron by the sterno-pleural suture. The posterior median margin is characterized by a triangular emargination on each side of which is a small rounded protuberance, the *coxal condyle*. A membrane attached along the posterior margin lines the antecoxal pieces forming the shallow ventral surface of the coxal cavity. The antecoxal pieces are very finely strigulated and bear a few setae in more or less linear arrangement along the width of the piece. The entire sternite anterior to the antecoxal portion is likewise reticulately strigulated and finely, densely punctured in the median area becoming more coarsely and less densely punctured laterally. There is a small area just anterior to the antecoxal pieces which is devoid of punctures.

The metathoracic pleuron is divided longitudinally by the *pleural suture* into the ventral episternum and the dorsal epimeron. The *episternum* is subrectangular. Its anterior edge lies under and articulates with the posterior edge of the mesepimeron. Posteriorly it partially overlaps the small *trochantin*. The surface of the episternum is quite thickly covered with U-shaped elevations and in the center of each elevation is a short seta. This type of vestiture and sculpture is lacking along the sterno-pleural suture, the pleural suture and the cephalic extremity of the sclerite. The surface is finely strigulated throughout.

The *epimeron* varies considerably in shape and degree of sclerotization from anterior to posterior. It extends distally beyond and around the posterior extremity of the episternum to form the coxal and trochantinal articulations. Except for this caudal extension the epimeron is concealed beneath the elytron. As the epimeron continues cephalically it becomes sub-membranous and finally combines with the metepisternal process to form the *pleural wing process*. Its dorsal aspect is joined to the metano-

tum by membrane. In the caudal sclerotized third, punctures and setae are sparsely distributed and also along the pleural suture in the caudal half of the sclerite. Minute strigulations cover the entire surface of the epimeron.

A ridge projects entally from the ventral metathoracic midline. Fused to its posterior extremity in the region of the coxal condyles is the *metendosternite* which extends cephalad as far as the anterior end of the median fold where it branches into the two *furcal arms.*

Metathoracic legs.—(Figure 16) The metathoracic legs are only slightly longer than the mesothoracic legs and closely resemble them except for the coxa and the four-segmented tarsi. The *coxa* is large and transverse. It articulates laterally with the metepimeron, antero-mesally with the coxal condyle of the sternum, and postero-mesally with the trochanter. An irregular punctate groove extends from the epimeral to the trochanteral articulation. The internal aspect of this groove appears to be a crescent shaped muscle disk. A second hemispherical muscle disk originates very close to the point of articulation with the coxal condyles of the sternum. The anterior aspect of the coxa is without punctures although finely strigose above and below the irregular groove. The median apex is punctured and bears a density of short setae. The fine strigulation continues on the posterior aspect and a few punctures extend upward onto the posterior median surface from the ventral punctate area. The tarsus of the metathoracic leg is composed of four segments; the basal segment is not quite as long as the remaining three segments together. The tarsus also differs from that of the mesothoracic legs in having more of the strong setae on the ventral aspect.

Flying wings.—(Figures 21 & 22) The metathoracic wings or flying wings are as long as the body, well developed and with only moderately reduced venation. The *costa* (C) is present as a short vein which ends about midway along the anterior margin of the wing. It is sclerotized basally and attached by membrane to the anterior aspect of the metanotum. Entally the costal margin articulates with the wing process of the metathoracic pleuron. Immediately posterior to the costa are the *subcosta* (Sc) and *radius* (R). These two veins are separate in the basal portion of the wing, become fused near the middle and continue distally along the anterior margin to the point of the concave wing fold near the apex. Basally the *first axillary sclerite* articulates with the Sc and the *second axillary sclerite* with the R. A short bar connects the R with the *cubitus* (Cu) just distad of the wing base. This connection is referred to as the *anterior arculus* and according to Forbes (1922) is a short sector of the *media* (M). The dorsal surface of the R in the region of the arculus is characterized by several small pores,

a feature which serves to identify the R in most beetles according to Blackwelder (1936). A *radial cross vein* (r) connects the anterior edge of the *radial sector* (Rs) to the fused R and Sc. The *radio-medial cross vein* (r-m) is present and distinct between the base of the Rs and the M. As is characteristic of the Polyphaga the base of the Rs is lost and the portion remaining proximad of the r-m is interpreted as the *radial recurrent vein* (Rr).

Posterior to the R is the M which has been lost in the basal half of the wing and united with the Cu near the apex. The convex principal fold of the wing runs very closely along the whole extent of the anterior edge of this vein to the posterior margin of the wing.

The Cu is a very distinct and complete vein in this species extending from the base of the wing to the apex. As mentioned above it fuses with the M near the apex of the wing. Close to its base but distad of the anterior arculus lies the short *cubito-anal cross vein* (cu-a). A convex fold runs along the ventral edge of the Cu for a short distance midway between the base and apex of the wing. This is the cubital fold.

The proximal portion of the *first anal* (1A) is lost except for a short projection from the Cu near its base. The vein connected to the Cu by the cu-a cross vein is taken to be the remainder of the 1A. It continues distally to the posterior margin of the wing giving off the a*nal arculus* midway along its course.

The remainder of the anals make up a rather distinct anastomosing network of veins. The first branch of the second anal is absent. The *second branch* of the second anal (2nd. A_2) is present, fused basally with the *third anal* (3A), and connected by the anal arculus to 1A. The *third branch* of the second anal (2nd. A_3) forms the apical border of the *wedge cell* (W) and then becomes confluent with the *first branch* of the third anal (3rd. A_1). A cross vein (2nd.-3rd. a) projects obliquely posterior from the 2nd. A_2 to join 3A and form the proximal border of the wedge cell. The *second branch* of the third anal (3rd. A_2) arises near the base of 3A and extends almost to the posterior margin of the wing. The convex anal fold runs diagonally from the wing base between 3rd. A_2 and the fourth anal to the wing margin. The *fourth anal* (4A) originates in close proximity to the *third axillary sclerite* and also appears to be nearly joined to the base of the 3A by a sclerotized area. It may actually be a branch of 3A but since the trachea does not traverse the connecting area, it is more likely the true 4A.

The wing folds discussed above indicate that the pattern is typical of the Heteromera and is therefore included in Series 2 of Polyphaga by Forbes (1926).

Various regions of the wing are irregularly marked with dark brown (the cross-hatched areas on Figure 21), and the entire costal area and

radial sector area are even darker brown than the remainder of the wing. Dorsally and ventrally the wing surface is densely covered with minute conical projections. These are particularly numerous and sharp in the apical and costal regions but become less numerous toward the center of the base and a little less pointed toward the base and posterior margin of the wing.

The wing articulates with the metanotum by means of the three axillary sclerites and the anterior and posterior notal wing processes. The first axillary sclerite articulates along its mesal edge with the anterior notal wing process. The posterior tip of the second axillary sclerite and the median protuberance of the third axillary sclerite articulate with the tip of the posterior notal wing process of the metanotum. The articulations of the axillary sclerites with the various wing veins and areas has been discussed above.

Abdomen

(Figures 23 and 24)

Tergite one is united anteriorly with the metathoracic postnotum and extends laterally to the large oval *spiracles*. There is no sternite for the first abdominal segment.

Tergite two is as wide and about twice as long in the center as the first and overlaps the third tergite broadly in the median area. The small, circular spiracle of the second segment is situated in the lateral membrane of the dorsum near the anterior border of the second tergite. *Sternite two* is reduced, fused with the third and membranous except for a small feebly sclerotized area on each side of the center. The membrane anterior to the fused second and third sternites is attached to the ental surface of the metathoracic coxae.

Tergite three is like the others and the size and location of the spiracle of this segment is like that of segment two as are those of segments four, five and six. *Sternite three*, fused with sternite two, is the longest and widest sternite in this species and has a deep V-shaped excavation anteriorly for the reception of the large transverse metathoracic coxae. The excavated area is feebly sclerotized and its anterior margin in general is not distinguished from the second sternite except by the gradual transition from light sclerotization to membrane. Just caudad of this point of fusion is a posteriorly directed fold or ridge which has the same shape as the ventral margin of the coxal excavation. This ridge marks the cephalic extent of the coxae. The center of sternite two plus three is not excavated but projects cephalad as the intercoxal piece.

Tergites four and *five* are very similar in length. The fifth is narrower as is each succeeding segment caudad of the third. *Sternite four* is as long

as sternite five. *Sternite five* has its postero-latero corners slightly produced caudally and its posterior margin is characterized by a narrow coriaceous edge.

Tergite six is narrower but longer than the one preceding it. It overlaps the seventh tergite but not by the ordinary membranous fold. A narrow glabrous strip extends from the caudal edge of the sixth tergite to overlap the anterior fold of the seventh. *Sternite six* has its posterior corners more produced than those of the fifth and a more extensive coriaceous posterior edge.

Tergite seven is the last one completely visible in a dorsal view. It is broadly and roundly tapered posteriorly, heavily sclerotized and its cephalic margin forms a shallow anterior fold. The lateral aspect of this tergite is deflected for about three-fourths of its length and just distad of the anterior margin this deflected portion is reflected dorsally again for a short distance. The *spiracle* of the seventh segment is smaller than any of the others and situated in the membrane between the tergite and sternite of this segment. *Sternite seven* is overlapped by the produced corners of the preceding segment. Its apex is more broadly rounded than that of the seventh tergite and in the female its median posterior margin is produced into a broad, shallow lobe with a very slight sinuation in the center. The median apical surface of this sternite is also broadly but shallowly impressed. Sternite seven of the male is described in the section on genitalia.

Tergite eight of the female is normally almost or completely withdrawn beneath the seventh. It is greatly reduced and composed of two feebly sclerotized plates which are in close proximity to each other distally but diverge proximally. They are joined to each other along the median edges by a membrane which continues anteriorly to the ventral surface of the seventh tergite. *Sternite eight* is reduced in size in the female. It is a single sclerite with a membranous base from which an *apodeme* arises and projects cephalically as far as the anterior half of the fourth segment. The apex of this sternite is truncate and very slightly sinuate. Sternite eight of the male is described in the section on genitalia. The eighth set of spiracles is present though small and difficult to see.

There are no paratergites between the tergum and sternum. The lateral margin of each sternite is reflected dorsally to form a narrow concave ledge which is connected to the membrane of the dorsum.

The sculpture and vestiture of the sternum is quite uniformly alike for segments three through six, finely alutaceous, dark brown, moderately punctate with short stiff setae, and a narrow glabrous posterior margin on each of these sternites. Each sternite seems to be faintly longitudinally

rugose. The margin of the apical lobe of sternite seven bears setae. Sternite eight is less distinctly alutaceous and has fewer punctures than the preceding segments. It bears a few scattered short setae over its surface and several longer ones of varying lengths along the apical margin.

The tergum is characteristically feebly sclerotized, very finely alutaceous and, except for the seventh tergite, devoid of punctures and setae. The anterior half of tergite seven is much like the preceding terga but the posterior half has the same type of sculpture and vestiture as is typical of sternites three through six. The setae become much longer and coarser at the posterior margin. The tergal plates of the eighth segment possess a few coarse punctures near the apices and a mixture of very long, medium and short setae in the same region.

Male genitalia

(Figures 25-27)

All the abdominal segments distad of the seventh in the male can be considered as modified to form the genitalia which are somewhat more specialized than those of the female of this species. However, the ninth segment is properly called the genital segment. The Tenebrionid type of genitalia is found in this species as in those species of Alleculidae discussed by Sharp and Muir (1912).

Tergite seven resembles that of the female but is sub-truncate apically. The posterior margin of *sternite seven* (fig. 24) has a distinct shallow but wide emargination. The spiracles of segment seven are as in the female.

Tergite eight of the male and female are similar although the tergal plates are somewhat larger in the male. This tergite is closely attached along its lateral edges to the dorsal surface of sternite eight. A membranous lip extends from the distal margin of tergite eight. The *rectum* passes over the dorsal surface of the basal piece of the tegmen with the *anal opening* directly ventral to this strip of membrane. *Sternite eight* is large, very prominent and bilobed distally to form two long, excavated, laterally flattened lobes. These lobes extend laterally along each side of the median lobe of the aedeagus. The apex of each lobe is set with short, stout setae. Long, fine setae border the distal median edge of the sternite. The eighth sternite is less heavily sclerotized proximad of the lobes and becomes membranous basally. The small spiracles of the eighth segment are present in the membrane between the tergite and the sternite close to the base of the ninth sternite.

Tergite nine is present in the male as an extremely reduced sclerite there being but a tiny plate on each side of the dorsal surface of the rectum just

proximad of the anus. The *sternite nine* is highly modified and composed of two arm-like processes united basally where they articulate with the base of the tegmen. The arms pass distally from this point, first, ventral to the basal piece of the tegmen, then lateral to it and finally the expanded apices pass dorsal to the base of the parameres in the region of the first connecting membrane. There are a few setae at the apex of each arm of the sternite. The two arms are joined to each other by membrane extending across the ventral surface of the basal piece.

The *tegmen* is made up of the basal piece plus the parameres. In this species the *basal piece* is long, slightly arcuate, sclerotized dorsally and membranous ventrally. The basal piece is attached proximally to the ninth abdominal segment and anus by the *second connecting membrane* and distally to the median lobe by the *first connecting membrane*. The first connecting membrane does not allow much movement between the basal piece and the median lobe. Two *apophyses* of the median lobe extend the length of the basal piece internally. The *parameres* have fused dorsally to form a conical plate. The edges turned under form a slit-like opening through which protrudes the *membranous median lobe* or penis.

The *ejaculatory duct* enters the ventral surface of the tegmen just distad of the base of the ninth sternite and extends along the length of the basal piece to the basal orifice of the median lobe. The median lobe bears the *ostium* on the dorsal apical surface through which the ejaculatory duct opens.

The aedeagus (tegmen plus penis) as here described corresponds to the Vaginate type discussed by Lindroth and Palmen (1956).

Female genitalia

(Figures 28 and 29)

The genitalia of the female are composed of the modified ninth and tenth abdominal segments. The eighth segment is reduced as described above.

The membranous *median oviduct* extends distad of the eighth segment and ends in the vagina. The median oviduct when retracted forms a telescoped tube with the distal portion drawn back into the proximal connecting membrane.

The *rectum* is situated dorsal to the median oviduct and has a large funnel-shaped *anal opening*. The median dorsal surface of the anus is a feebly sclerotized area which becomes a narrow strong rod for a short distance cephalad. The lateral plates located ventral to the anus represent the halves of the ninth tergite and are referred to as the *valvifers* by Tanner (1927).

The bulbous terminal portion of the median oviduct is the *vagina* which has an apical orifice, the *vulva*. The *hemisternites* or halves of the ninth sternite partially surround the vagina and extend a short distance beyond its apex. A *stylus* extends laterally from near the apex of each hemisternite.

Discussion

There are a number of problems involving the correct interpretation of the morphological structures of Coleoptera.

One of the more controversial points concerns the pterothoracic sternites. Ferris (1940) speaks of the non-existence of such structures in beetles. There was no difficulty in using the so-called orthodox interpretation of the sternal elements in the species here studied, but there is a problem, at least in the minds of some, of applying this same interpretation throughout the order.

In consulting the work of Tanner (1927) and Lindroth and Palmen (1956) on the female genitalia the difficulty of inconsistency and disagreement in interpretation of structures was met again. Furthermore, anyone who has investigated beetle morphology at all is aware of the fact that a better understanding of the whole female reproductive system is much needed. Such knowledge may well supply useful taxonomic characters.

Snodgrass (1909) wrote that the trochantin is absent on the metathorax of Coleoptera. Campau (1940) found an exception to this statement in the family Cupesidae which he considered to be probably the only exception. In this study of *Capnochroa fuliginosa* (Melsh.) a trochantin was found on the metathorax and mesothorax but not on the prothorax.

No attempt will be made here to remove or resolve these basic Coleopteran problems but it can be concluded that the very existence of them and the lack of equivalence in the views held by different workers is proof enough that a complete, careful and comprehensive morphological study of the whole order, Coleoptera, is very much needed if the systematic work on beetles is to achieve any semblance of a valid scheme of natural classification.

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List of abbreviations

A, dorso-lateral acetabulum
a, acetabulum
Ac, antecosta
Aclp, anteclypeus
acs, antecostal suture
Acx, antecoxal piece
An, anus
ANP, anterior notal wing process
AntR, antennal ridge
apo., apodeme of sternite 8
apo.p., apophyses of median lobe
AT, anterior tentorial arms
1Ax, *2Ax*, etc., axillary sclerite
AxC, axillary cord
Ba, basalare
b.pc, basal piece
C, ventro-lateral condyle
c, condyle
Cc, calcaria
Cd, cardo

Clp, clypeus
CLR, clypeolabral ridge
cm1, *cm2*, connecting membranes
Cr, crassa
Cx, coxa
CxC, coxal cavities
Cxc, coxal condyle
Dr, dorsal ridge
DT, dorsal tentorial arms
du.ej., ejaculatory duct
E, eye
Emp, empodium
Endst, metendosternite
Ephy, epipharynx
EPlf, epipleural fold
Epm, epimeron
Eps, episternum
es, epistomal suture
Fm, femur
For, foramen magnum
Fr, frons
Fu, furcal arms
Ga, galea
Ge, gena
Gu, gula
Hphy, hypopharynx
Hpm, hypomera
HS, hypopharyngeal suspensorium
Lc, lacinia
Lig, ligula
m, *m1*, median plates
ma, molar area
Mt, mentum
no, convergent sutures
o, ostium
Oc, occiput
oc, oculata
ocs, occipital suture
ovc, median oviduct
P, prostheca
p, median lobe
Pge, postgenae
Plf, palpifer
Plg, palpiger
Plp, palpus
PlR, pleural ridge
PlS$_2$, *PlS*$_3$, pleural sutures
pm, parameres
Pmt, postlabium
PN, postnotum
PN$_3$, postnotal plates
PNP, posterior notal wing process
Prlb, prelabium
Prmt, prementum
Prp, prepectus
Prsc, prescutum
PT, posterior tentorial arms
pt, posterior tentorial pits
Rect, rectum
S1, *S2*, *S3*, *etc.*, sternites
S9, hemisternites
SA, sternal apophyses
Scl, scutellum
Sct, scutum
Sge, subgenal area
SgR, subgenal ridge
sgs, subgenal suture
Smt, submentum
sns, sterno-notal suture
Sp, spiracles
Spls, sterno-pleural suture
Ss, spinasternum
St, stipes
st, stylus
T1, *T2*, *T3*, *etc.*, tergites
T9, valvifers
Tar, tarsus
TB, tentorial bridge
Tb, tibia
tm, tegmen
Tn, trochantin
Tor, tormae
Tr, torchanter
Un, claws
Utr, unguitractor plate
vag, vagina
vs, scutoscutellar ridges
vu, vluva
Vx, vertex
W, wedge cell
WP, pleural wing process
x, tendon of retractor muscle

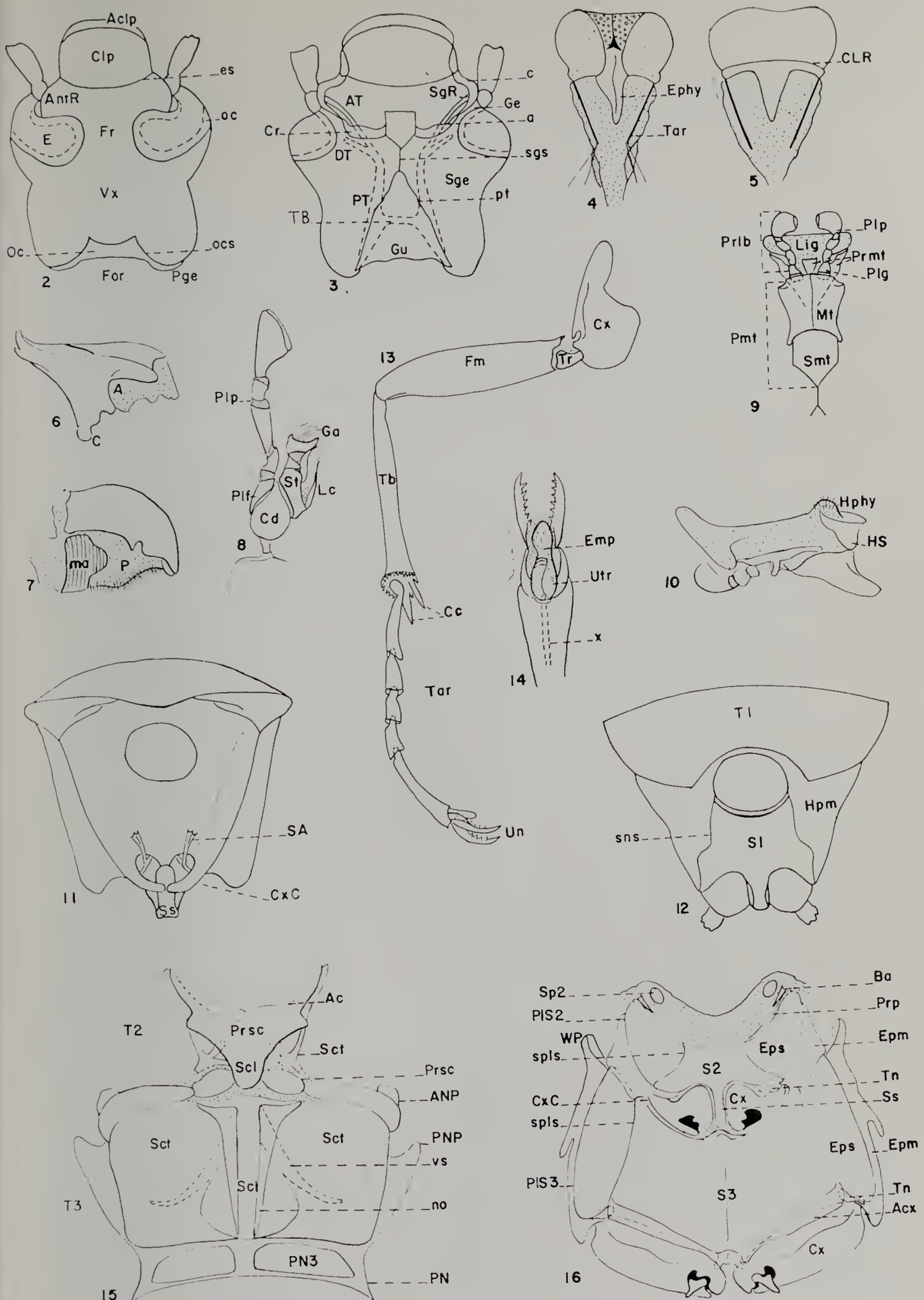

Fig. 2.—Head capsule, dorsal; fig. 3.—Head capsule, ventral; fig. 4.—Labrum, ventral; fig. 5.—Labrum, dorsal; fig. 6.—Left mandible, lateral; fig. 7.—Left mandible, dorso-medial; fig. 8.—Right maxilla, ventral; fig. 9—Labium, ventral; fig. 10.—Labium, dorso-lateral; fig. 11.—Prothorax, posterior; fig. 12.—Prothorax, anterior; fig. 13.—Prothoracic leg; fig. 14.—Detail of fifth tarsal segment; fig. 15.—Pterothorax, dorsal; fig. 16.—Pterothorax, ventral.

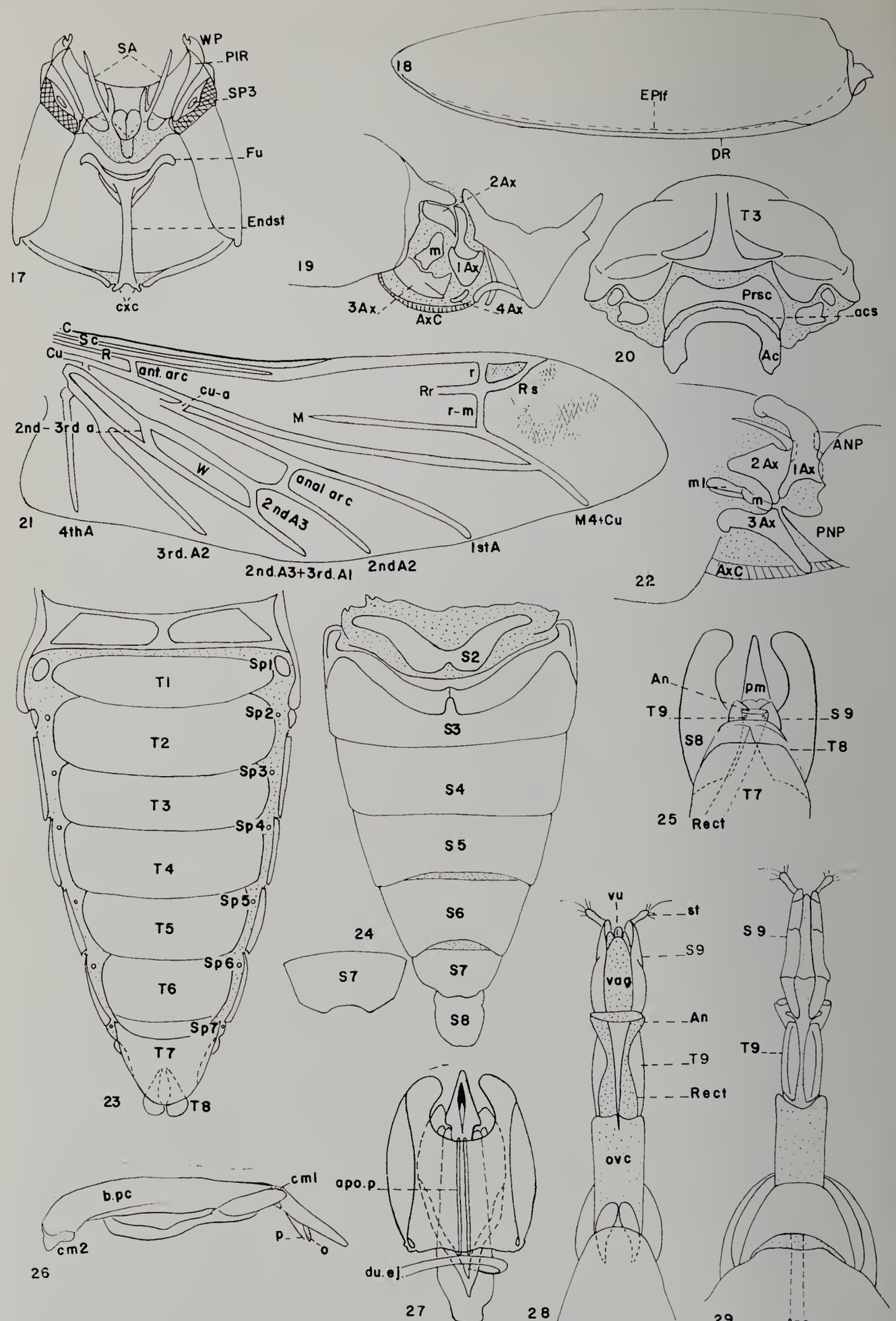

FIG. 17.—Pterothoracic endoskeleton; FIG. 18.—Elytron, right; FIG. 19.—Articulation of elytron; FIG. 20.—Metathorax, anterior; FIG. 21.—Flying wing; FIG. 22.—Articulation of flying wing; FIG. 23.—Abdomen, dorsal; FIG. 24.—Abdomen, ventral; inset: S7 of male; FIG. 25.—Male genitalia, dorsal; FIG. 26.—Tegmen, lateral; FIG. 27.—Male genitalia, ventral; FIG. 28.—Female genitalia, dorsal; FIG. 29.—Female genitalia, ventral.